

STUDIES ON THE PARASITES OF THE TER-
MITES I. ON *STREBLOMASTIX STRIX*, A
POLYMASTIGOTE FLAGELLATE WITH
A LINEAR PLASMODIAL PHASE

BY

CHARLES ATWOOD KOFOID AND OLIVE SWEZY

CONTENTS

	PAGE
Introduction	1
Material	2
Technique	3
Occurrence	4
Morphology	4
Size and shape of body	5
Cytoplasm	7
Neuromotor apparatus	7
Direction of torsion	9
Nucleus	10
Binary fission	10
Multiple fission	12
Adaptations	13
Relationships	14
Summary	16
Literature cited	17
Explanation of plates	18

INTRODUCTION

One of the most curious and unique faunal associations to be found among the parasitic Protozoa is the group parasitic or commensal in the intestinal tract of the social termites. These parasites are remarkable not only for the vast numbers that may be found within a single host, but also for the degree of development and specialization which distinguishes many of the species. This is especially true of the

forms belonging to the family Trichonymphidae, such as *Trichonympha* Leidy, which are among the most highly specialized members of the Protozoa.

Along with these more complex forms are others which, while simpler in structure, yet show certain peculiar morphological characteristics that distinguish them as a group apart from other intestinal flagellates. Among these we find *Pyrsonympha vertens* and *Dincnympha gracilis* described by Leidy in 1881.

Later investigators have added both to the number of genera and of species of these peculiar flagellates.

MATERIAL

The material for these studies was obtained from one species of termite which is abundant on the University campus at Berkeley. This is *Termopsis angusticollis* Walker and was identified for us by Dr. Nathan Banks of the Museum of Comparative Zoology at Cambridge, Mass. Most of this material was obtained from the decayed trunk of an oak tree in Strawberry Cañon. Many of the same species were obtained during the swarming season from the piles on Meiggs Wharf, San Francisco, by Dr. A. D. Drew of the Public Health Service.

These termites are large and show an infection of about one hundred per cent, soldiers, workers and males of the colony being infected alike. The amount of infection in a single individual is relatively enormous. The abdomen is large and nearly filled by the greatly swollen intestine. This distension is caused by the vast numbers of parasitic and commensal protozoans which fill the lumen of the intestine. When this is opened a thick milky fluid exudes. Under the lens this is found to be composed of great quantities of these small forms, thickly massed together, along with fragments of wood upon which the host, as well as some of its commensals, feeds.

In *Termopsis angusticollis* four different species of large protozoans are invariably present, sometimes about equal in number or with one predominating over the others. In addition to these there are usually present minute forms of two, sometimes three different species of flagellates, the whole forming a complex of organisms wonderful both for variety and amount. Of these forms the two largest species belonging to the family Trichonymphidae and a third species belonging to the Polymastigidae, will be reserved for discussion in later

papers. In the present paper the fourth member of this group, also a polymastigote flagellate, will be considered, with a discussion of its morphology, relationships and life history in so far as they have been determined.

TECHNIQUE

The flagellates found in the termites are exceedingly delicate. Great difficulty has been experienced in keeping them alive for continuous observation under the microscope for any length of time. The use of distilled or tap water resulted in the complete dissolution of the larger flagellates in a few minutes. The smaller ones would survive a somewhat longer period. Various other culture media were tried, such as Ringers' solution, normal salt solution, malted milk and the white of egg. Of these the last one was the most successful, a few flagellates surviving in the culture at the end of twenty-four hours. These cultures were made with a hanging drop or with a greater amount of fluid in a deep culture slide.

Intra vitam stains, such as neutral red, Janus green and new methylene blue G G, were used. Of these neutral red gave the best results.

The methods of fixing and staining which have been found the most satisfactory were those outlined by us in previous work on parasitic flagellates (Kofoid and Swezy, 1915), that is, a modified Heidenhain's iron haematoxylin following fixation in hot Schaudinn's fluid. Other stains as well as various fixing agents were tried, both with smear preparations and with sectioned material. In the latter cases two methods were followed. In the first the entire abdomen of the termite was used, fixed in Schaudinn's or strong Flenning's solution. In the second the intestine was teased out in a drop of normal salt solution and then placed in the fixing fluid. These sections were stained with haematoxylin or with a modified Mallory's connective tissue stain (Yocom, 1918).

Considerable difficulty has been experienced in making good preparations of this material by the ordinary smear methods. The exceeding delicacy of the various flagellates results in distortions of the body and breaking down of its cytoplasmic organization. This is usually confined to the posterior end, leaving the anterior end, nucleus and motor organelles intact. This difficulty was partly overcome by using albumen fixative on the cover slip and diluting the contents of the

intestine with a small drop of normal salt solution before making the smear. The material thus treated may be spread with less mechanical injury and the albumen prevents the great loss of organisms that would otherwise occur when it is placed in the fixing fluid. The addition of albumen, however, necessitates quick work in making the preparations, to prevent the death of the organisms through its action rather than that of the fixing fluids.

OCCURRENCE

These flagellates are more restricted in their occurrence in the intestine of the host than are the other forms which are present with it. They are seldom found far away from the mucus of the epithelium, usually attaching themselves to it (pl. 1, fig. 9) by means of the holdfast-like anterior end of the body. They may be seen completely filling the folds of the wall of the intestine with the posterior portion projecting into the lumen of the canal.

Near the anterior part of the posterior region of the intestine, immediately behind the origin of the malpighian tubules, a slight enlargement of the intestine may be noted, with one side marked by two lines of constriction passing backward for a short distance. This forms a rounded chamber marked off from the main portion of the canal. In cross-sections this may be found completely filled with *Streblomastix*, a dense coating of the flagellates attached to the wall and others filling the remainder of the cavity. Plate 2, figure 8 shows a small portion of the wall in this region with a few only of the attached flagellates.

These flagellates occur much less frequently in other parts of the posterior and mid-regions of the intestine, but when present are always restricted to the peripheral zone with the larger flagellates occupying the remainder of the lumen. They have been found in nearly seventy per cent of the hosts examined.

MORPHOLOGY

Streblomastix is profoundly a linear organism. Elongation dominates all of its organelles in adaptation to its crowded grouping in its parasitic habitat. This elongation affects not only the body as a whole but also the nucleus, rhizoplast, and flagella, and pervades not only the normal vegetative trophozoite, but also the gigantic over-

grown and possibly abnormal phases occasionally found. The linear form of body and also of nucleus continues not only during the trophozoite phase but likewise, in so far as we have seen the stages, during both binary and multiple fission. During multiple fission itself the organism becomes a greatly elongated thread with its nuclei stretched lengthwise as a constricting thread in the axis of the body. All trace of rounding up or sphericity seems thus to have been banished utterly from both body and nucleus at all stages of its life cycle.

SIZE AND SHAPE OF BODY

The body is ordinarily elongate fusiform, tapering subequally at the two ends. Either or both ends (pl. 1, figs. 1, 7) may be somewhat blunt but the usual form of the anterior end is a slender cone while the posterior one may have a trifle more convexity. Its length is generally from twelve to sixteen times its greatest diameter which is found near the middle of the body. The shorter individuals (pl. 1, fig. 5) may be only six times the diameter. These are evidently recent schizonts. On the other hand, giant individuals, which are possibly approaching multiple fission (pl. 2, fig. 13), may be thirty times their diameter in length, and the "plasmodial" stage of multiple fission (pl. 2, fig. 14) attains a length as much as seventy times its own diameter. Measurements of two hundred individuals gave a frequency curve with a marked left-hand skew with the mode at 40μ and the extreme range in length of from 20 to 530μ . One-half of the individuals were included between 20 and 80μ . The longest individuals included those in which multiple fission was in progress and it is probable that the others were approaching that phase.

The contour of the body is not a smooth line, for the surface is traversed by spiral ridges with furrows between, giving it the form, except for its taper, of the shaft of a Norman Romanesque column. These ridges are four in number, broadly convex and equidistant and they wind about the body from the anterior end posteriorly from the left over to the right. It is thus like a left-hand screw if the anterior end is regarded as the tip. The steepness of the spiral varies with the length of the organism, its contraction, and the phase of the life cycle. In late stages of binary (pl. 2, fig. 17) and multiple fission (pl. 2, fig. 14) much of the torsion is relaxed. In stages which may be prior to binary fission (pl. 1, fig. 7; pl. 2, fig. 10) these may be

three to five turns, and a giant individual, presumably preceding multiple fission (pl. 2, fig. 13), has eight turns. Normal vegetative individuals (pl. 1, figs. 1, 6, 8) have one to two turns only.

The grooves between the ridges mark the location of ectoplasmic lines of deeply staining material, possibly myonemes, or extensions

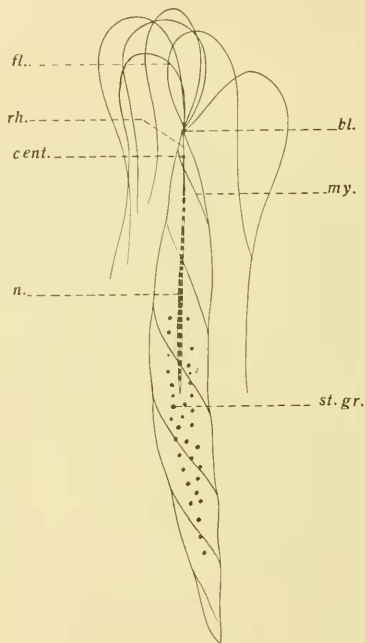


Fig. A. Semidiagrammatic figure of *Streblo mastix strix* gen. nov., sp. nov. Black granules in cytoplasm show particles stained *intra vitam* with neutral red. Abbreviations: *bl.*, blepharoplast; *cent.*, centrosome; *fl.*, flagella; *my.*, myonemes; *n.*, nucleus; *rh.*, rhizoplast; *st. gr.*, stained granules. $\times 2000$.

of the neuromotor system. They are feebly stained, if at all, in binary and multiple fission (pl. 2, figs. 14, 17, 19) and are sometimes marked by accumulations of minute granules staining black with haematoxylin. They terminate anteriorly at or near the blepharoplast and fade out posteriorly.

CYTOPLASM

The cell contents are undifferentiated. No separation of ectoplasm, pellicle, and endoplasm is visible. There is no cytostome and no food particles or food vacuoles have been detected. There is no contractile vacuole visible. The only differentiated structures normally visible in the organism are the nucleus and the neuromotor apparatus. However, on treatment with neutral red (fig. A) certain granules became stained in the axial cytoplasm in the posterior two-thirds of the body, indicating an endoplasmic territory within which digestion of the absorbed food was in progress.

NEUROMOTOR APPARATUS

This neuromotor apparatus consists of a centrosome, rhizoplast, blepharoplast, myonemes, and six flagella. The centrosome (fig. A, *cent.*; pl. 1, fig. 9; pl. 2, fig. 10) is found at the anterior tip of the elongated nucleus. It appears to be a spherical granule in or on the nuclear membrane. It is temporary or evanescent and does not appear to play any visible part in either binary or multiple fission. It is quite possible that the granule thus interpreted is a mere temporary accumulation of chromatoidal substance on the rhizoplast without morphological meaning. Its position with reference to nucleus, rhizoplast and blepharoplast is similar to that of the centrosomes in *Giardia* (Kofoid and Christiansen, 1915, and Boeck, 1917) hence the designation suggested. It may be that the extrusion of the rhizoplast serves to bring the structure into view from a more intimate union with the nuclear membrane.

The rhizoplast (fig. A, *rh.*) is a slender, deeply staining thread running anteriorly from the centrosome or the anterior tip of the nucleus to the blepharoplast. Its length ordinarily is about equal to the greatest diameter of the body and the line of demarcation between the attenuate end of the nucleus and this thread is often not readily determined. There is a probability that this is more or less contractile, as is seen on a comparison of our figures. In one instance (pl. 1, fig. 7) this structure appears to be foreshortened and thickened, by contraction, onto the anterior end of the nucleus.

One remarkable feature of this structure is its capacity of being extended beyond the anterior end of the body as a long spike bearing the blepharoplast and its attached flagella at its tip. A con-

siderable increase in length to nearly three or even six times the normal seems possible (pl. 1, fig. 3). No evidence of an extension of the protoplasmic pellicle to form a sheath for this remarkable organ has been found. It may also be so foreshortened that the blepharoplast and centrosome are brought into close juxtaposition (pl. 1, fig. 2).

In view of the fact that the individuals lie closely packed against the digestive epithelium with the blepharoplast thrust against the epithelial cell of the host, it appears that this protrusible organ serves in some way as a part of a somewhat adjustable holdfast. We have no evidence that it can be or is ever thrust into the body of the cell, though such a mode of attachment seems possible.

The blepharoplast (fig. A, *bl.*) is a sphere at the anterior end of the rhizoplast about 0.5μ in diameter. The six flagella spring directly from it. It lies normally in the extreme anterior end of the body and is carried out with the extruded rhizoplast. The possibility of its being drawn out in detaching the parasite from its adhesion to the cells of the host is not precluded, but the numbers of such cases and the retention of normal symmetry of both body and rhizoplast does not support the suggestion of forceable extraction:

In one instance (pl. 1, fig. 4) a terminal blob of cytoplasm with a deeply staining terminal cap is attached to the side of the blepharoplast, and in another a considerable mass of protoplasm lies about the extruded blepharoplast. While these may be abnormalities it is possible that under certain conditions the cytoplasm assists locally in the holdfast function of the blepharoplast by forming an enlarged mass about it.

The six flagella are equal, habitually trailed posteriorly and about half as long as the body. They serve to keep up the circulation of the fluid contents of the digestive tract as they lie parallel to the closely packed bodies of the parasites (pl. 1, fig. 8) in the folds of the digestive epithelium.

The four peripheral spiral threads (fig. A, *my.*) which terminate at or near the blepharoplast must be regarded as a part of the neuromotor apparatus. Their relations to the blepharoplast and their stainability as well as the homology suggest this. Their function, if contractile (and their spiral course indicates this), appears to be to force the blepharoplast into intimate contact with the cells of the host. They persist at cytolysis and individuals are often found (pl. 1, fig. 10) in which these myonemes are frayed out as distinct lines.

These myonemes are evidently quite firm fibers, somewhat elastic and more or less rigid. They often stain very deeply especially in disintegrating individuals (pl. 1, fig. 1).

DIRECTION OF TORSION

The direction of torsion of these elements of the neuromotor apparatus is not without a deep significance. It is the same as that of the undulating membrane or attached flagellum of *Trichomonas*, *Trichomitus*, *Tetratrichomonas* and *Eutrichomastix* (Kofoid and Swezy, 1915), other polymastigotes in which torsion finds some structural expression. This same direction of torsion appears in the myonemes of *Pyrsonympha* and *Dincnympha* (Leidy, 1881). Grassi and Sandias (1893) reverse the direction of *Pyrsonympha* and of *Holomastigotes* in their figures, while Porter (1897) figures both directions. It is perhaps significant that his figures from life have the reversed direction while those from preparations, and therefore presumably accurate, have the normal leiotropic, or to be expected, direction. The reversals figured by Grassi and Sandias require confirmation before acceptance. The *Pyrsonympha* of this contribution (1893) is later designated as *Spirotrichonympha* by Grassi and Foà (1911) but without note of the differences in torsion. Zulueta (1915) figures the leiotropic direction in what appears to be Grassi's *Spirotrichonympha*. While it is quite possible that both leiotropic and dextrotropic genera or species exist, or that functional reversals of torsion occur in the individual it is even more evident that critical observations are essential to establish these diametrically opposed conditions. Pending such investigations the preponderance of the evidence favors the view that the torsion of the more primitive Trichonymphidae is leiotropic, that is from right over to left posteriorly, as it is in *Streblomastix*.

This is also the fundamental direction of the girdle and of the encircling transverse flagellum of the Dinoflagellata, and also of the attached collar-forming, ribbon-like flagellum of the Craspedomonadina (Burek, 1909). These facts are suggestive of an extensive and deep-seated leiotropism in the organization of the Mastigophora which finds expression in both externally attached flagella and internal contractile myonemes. That it may be conditioned by some equally pervasive stereometric properties of certain compounds of the living substance seems plausible.

NUCLEUS

The nucleus (fig. A, *n.*) shares the elongation which affects the body and appears to be pulled far anterior by the holdfast function of the blepharoplast so that in comparison with other polymastigotes its location is exceptionally far anterior. Its length is from 0.3 to 0.5 that of the body itself and its shape is fusiform but much more slender than the body, its length being fifteen to twenty-five times its diameter. It tapers about equally at both ends and appears in most of our preparations as a solid black axial strand in the anterior part of the body. Unless very strongly decolorized no internal structures can be made out. It appears to be composed of almost solid chromatin. When sufficiently decolorized (pl. 1, figs. 7, 9) a distinct nuclear membrane is evident within which a single row of black chromatin spherules, decreasing in size towards each end, can be detected. These are not uniform in size or arrangement and are about twenty-five in number. They are not unlike the chromomeres which we have found in the chromosomes of *Trichonympha*.

BINARY FISSION

The life history of *Streblomastix* presents those phases of development which we (Kofoed and Swezy, 1915 and Kofoed and Christiansen, 1915) have previously described for other polymastigotes, namely, binary and multiple fission. As yet no encystment has been detected and no indications of sexual reproduction. The differences in size which we find would doubtless some years ago have afforded a basis for the speculative designation of microgametes and macrogametes and the corresponding gametocytes as well as for the predication of sex, as Hartmann (1910) did in the case of *Trichonympha*. However, in the absence of evidence of *sexual behavior* and observed fusion of gametic nuclei, the free swing of such speculation is wisely held in abeyance.

Binary fission occurs in the trophozoite stage. There is some evidence that it is cyclic since many individuals in approximately the same stage of mitosis will be found in a single host. It is not, however, restricted wholly to such cycles since isolated cases of fission have been found and not all individuals parasitic in one host are in fission at one time. Successive infections and diverse stocks of the parasites doubtless exist in the host and may afford the occasion for this diversity.

Unfortunately our material, though extensive, has not given us all of the stages of nuclear behavior during fission so that we are unable to trace wholly, the successive phases of mitosis. We have found no clear evidence of chromosome formation, beyond the twenty-five or more spherical aggregates of chromatin in the linear nucleus. We have found no spherical stage of the nucleus, no skein, and have not detected the division of the blepharoplast which doubtless occurs, neither have we been able to find the parademesma spun out between the daughter blepharoplasts (pl. 2, figs. 12, 13).

The process of binary fission, in so far as our partial evidence goes, takes place without any rounding-up of the elongated body. The anteriorly located blepharoplast divides, new flagella arise from one or both of the daughters, and one migrates to the opposite end of the body (pl. 2, fig. 11). In the meantime the nucleus has become greatly elongated, reaching from end to end of the body. It then constricts at the middle (pl. 2, fig. 12), finally parts there (pl. 2, fig. 19) and the two schizonts separate. To all appearances this is *transverse division*. Longitudinal division is, however, the fundamental and universal method of binary fission in the Euflagellata as compared with the Ciliata in which transverse division occurs. This seeming departure from the normal is, however, more apparent than real, for if the anterior blepharoplast divides and one daughter migrates to the posterior end we will have such an arrangement of schizonts as in *Trichomonas* after mitosis but before plasmotomy (Kofoid and Swezy, 1915, pl. 4, fig. 39). This is a temporary relation in such a metabolic form as *Trichomonas* but a more lasting one in *Streblomastix*. The mode of division is therefore still morphologically longitudinal though almost the last vestige of the appearance of that type of division has been submerged by the dominating elongation of the body in *Streblomastix*. While it is possible that there is a series of skein-chromosome changes in the nucleus which has escaped us, our present evidence indicates that these are also suppressed or hidden in the dense chromatin threads which part by simple median constriction (pl. 2, fig. 12). This parting is delayed until the posterior daughter blepharoplast is in its final position, as in other polymastigotes (Kofoid and Swezy, 1915). The frequent occurrence of stages in schizogony with the nucleus as yet undivided or dividing, but the neuromotor organelles in duplicate, indicates that both nuclear constriction and plasmotomy following thereon are prolonged processes.

MULTIPLE FISSION

Multiple fission in *Streblo mastix* is a cyclic process occurring in many individuals in a single host at one time. A few only may be found in this stage, or, in some instances, at least, the majority of individuals may be in the multinucleate phase.

This condition is preceded by the growth of the schizont from the small size resulting from multiple (pl. 2, fig. 13) or binary (fig. 17) fission to a much larger or even giant stage (pl. 2, fig. 13), which may be as much as twenty-six times the length of the smallest schizont. The body may have as much as sixty times the mass of the smallest stages. The nucleus, however, does not increase proportionately, remaining, in fact, at least in many instances, almost unchanged (pl. 2, fig. 13).

At some period during this increase in size multiple fission sets in. Not all trophozoites entering upon it attain the maximum size as will be seen on a comparison of figures 15 and 16 on plate 2. It is possible that figure 16 represents only a detached section of a larger plasmodium which is fragmenting, or it may be a small trophozoite in the initial stages of multiple fission.

Contrary to the behavior of the blepharoplast-flagella complex in binary fission where it leads in division, preceding the nucleus, we find that in multiple fission nuclear division by transverse constriction is taking place prior to the division of the blepharoplast (pl. 2, figs. 14, 15). The type of nuclear division is the same as in binary fission. We have not seen stages of multiplication of the blepharoplast or of plasmotomy.

The linear form persists during the period of multiple fission and the nucleus becomes an elongated axial chromatin thread which becomes attenuate locally and parts transversely (pl. 2, figs. 13-16). The number of nuclear segments varies, probably in a 2-4-8 sequence, although irregularities in this are apparent. The largest number observed is eight. This accords with multiple fission in other polymastigotes (Kofoid and Swezy, 1915; Kofoid and Christiansen, 1915).

There is some evidence that this stage is contractile and that when foreshortened the nuclei slip by one another. This is not a common condition and probably does not represent a rounded-up condition obligatory for multiple fission but rather a passing response to stimulus resulting in contraction.

Multiple fission stages which we have seen provide for eight schizonts when the plasmodium parts by plasmotomy into its constituent zooids. From irregularities in the number of nuclei in preparations in which multiple fission is common, it seems probable that plasmotomy is an irregular dropping off of individuals or groups of individuals from the common mass as in *Trichomonas*. We have no evidence as to the presence of a centrosome during multiple fission and none as to the origin of the new blepharoplast-flagella complexes of the daughter schizonts.

ADAPTATIONS

Although seemingly simple in structure *Strcblomastix* presents a series of structural adaptations which in the light of its parasitic mode of life become significant of intimate correlations with the conditions under which it exists and its habits. The entire loss of the cytostome is associated with feeding by osmosis and results in the disappearance of the bilateral asymmetry characteristic of polymastigotes such as *Trichomonas*. The absence of large food particles makes possible the elimination or reduction of cyclosis of the endoplasm and facilitates the change of form to a long and relatively very narrow spindle within which such movement would be impeded. The spiral course of the myonemes or spiral striae provides a most effective form of mechanism for an energetic thrust of the holdfast blepharoplast against or into the cells of the host. It is also a form of contraction which would disturb but slightly the closely packed grouping of the parasites. The spirally fluted surface combined with the action of the posteriorly directed flagella would give rise to vortex currents of the circumambient digestive fluids and thus provide the circulation essential to the metabolism of the parasite while at the same time permitting their segregation apart from the other organisms of the digestive tract of the host. The contractile extrusible rhizoplast-blepharoplast complex with its blob of cytoplasm affords an efficient structural holdfast. The elongation of the nucleus provides a spatially advantageous grouping for the nucleo-cytoplasmic interchanges in the absence of marked cyclosis.

The neuromotor apparatus is so arranged as to give well distributed contact with the surrounding medium by means of flagella and striae and with the host by means of the blepharoplast-rhizoplast, while this in turn is connected with the nucleus, thus establishing the structural essentials for efficient coördination of functions.

Even the reproductive phases of binary and multiple fission retain the elongated form characteristic of the trophozoite, thus permitting those stages to retain their position among the segregated parasites of their own kind. In other polymastigotes, such as *Trichomonas*, the stage of multiple fission is an amoeboid plasmodium, a rounded-up, somewhat shapeless amoeboid mass (Kofoid and Swezy, 1915). In *Strcblomastix*, however, the linear form persists throughout this phase, in so far as we have observed it, although it shows greater laxity of form and less torsion (pl. 2, figs. 14, 15) than do the vegetative trophozoites. Thus in every feature of its structure and phase of its life history *Strcblomastix* is intimately adapted to its peculiar parasitic mode of life notwithstanding its seeming simplicity of structure.

RELATIONSHIPS

The presence of six flagella definitely allocates *Strcblomastix* in the Order Polymastigina. Its relative simplicity of structure as compared with most genera of this order is shown by the undifferentiated condition of the flagella. There is no single specialized trailer attached as an undulating membrane, and none intracytoplasmic as an axostyle.

The presence of the four longitudinal spiral ectoplasmic "myonemes" or extensions of the neuromotor apparatus is very suggestive of a relationship to the Trichonymphidae in most of which such lines arise from the blepharoplast and are the stems from which spring the many so-called cilia. This relationship will be more evident on detailed comparison. There are eight such lines in *Dincnympha gracilis* (Leidy, 1881) along the course of each of which small cilia take their origin, but there are no developed anterior flagella. Zulueta (1915) has shown that these extend posteriorly as free flagella and that they are grouped four and four on the daughter centrosomes at the poles of the spindle at mitosis. The species upon which Zulueta worked appears to be the same as that figured by Grassi and Sandias (1893, pl. 5, figs. 18-20) which Grassi and Foà (1911) later distinguish from Leidy's species as *Spirotrichonympha*. *Pyrsonympha vertens* (Leidy, 1881 and Porter, 1897) likewise has eight such lines arising from the blepharoplast with small lateral cilia arising from them. Anteriorly there is a blepharoplast from which a free slender thread extends anteriorly into the host cell not unlike the rhizoplast-blepharo-

plast of *Streblomastix* in superficial appearance, but possibly homologous with flagella and derived by modification from one or more of them. There are four such lines in *Holomastigotes* (Grassi and Sandias, 1893) giving rise to lateral cilia and pursuing a spiral course posteriorly from what is probably an anterior blepharoplast. There are, however, no large anterior flagella arising from this point.

The form most nearly allied to *Streblomastix* appears to be *Pyrsonympha* by reason of the persistence of an anterior outgrowth from the blepharoplast which may be homologized with flagella. However, it has lateral cilia arising from its spiral lines. These *Streblomastix* entirely lacks. This absence of the lateral ciliary coat justifies the exclusion of *Streblomastix* from the Trichonymphidae and renders its retention in the Polymastigina necessary. However, it may be regarded as closely related to that branch of the polymastigote stock from which the Trichonymphidae originated. *Streblomastix* thus forms a living link between the Polymastigina and the Trichonymphidae, linking the latter seemingly aberrant forms more closely and definitely than heretofore to the Flagellata as its most highly specialized order.

It is obvious that *Streblomastix* can not be allocated in the family Hexamitidae and that its relationships with the Polymastigidae are relatively remote. Even its inclusion in the Polymastigina is somewhat problematical. Its transfer to the Trichonymphidae is defensible but requires a profound modification in the definition of that order. To set forth more strongly its intermediate position we have left it in the Polymastigina and propose for it a new family, the Streblomastigidae, as follows:

Family Streblomastigidae fam. nov.

Polymastigina with spiral myonemes and anterior flagella.

Streblomastix gen. nov.

Streblomastigidae with six anterior flagella and four leiotropic myonemes. Type species *Streblomastix strix* sp. nov. from *Termopsis angusticollis* Walker.

SUMMARY

1. *Streblomastix strix* occurs as an intestinal parasite of the termite *Termopsis angusticollis* and is usually found attached to the epithelium of the intestine posterior to the malpighian tubules, segregated from the other parasites in the lumen.

2. It is a linear organism with the nucleus elongated to conform to the shape of the body. Its neuromotor apparatus consists of centrosome, blepharoplast, four myonemes and six flagella, connected with the nucleus by the rhizoplast.

3. Binary fission apparently occurs without spindle formation. The nucleus elongates and becomes constricted prior to the constriction of the protoplasmic body.

4. Multiple fission is a cyclic process occurring in many individuals in a single host at one time. It may be preceded by the formation of giant individuals. The body retains its linear formation throughout the process as in binary fission. The nucleus elongates and constricts into daughter nuclei. The greatest number observed is eight.

5. The shape of the body and the arrangement of its neuromotor apparatus show striking adaptation to the habitat in which the flagellate is found and to its parasitic mode of life.

6. *Streblomastix* forms a living link between the Polymastigina and the Trichonymphidae but without close relations in either group. We therefore propose for it a new family, Streblomastigidae, which we place in the Polymastigina.

*Zoological Laboratory, University of California,
Berkeley, California.*

Transmitted September 5, 1918.

LITERATURE CITED

BOECK, W. C.

1917. Mitosis in *Giardia microti*. Univ. Calif. Publ. Zool., 18, 1-26, pl. 1.

BURCK, C.

1909. Zur Kenntnis der Histologie einiger Hornschwämme, sowie Studien über einige Choanoflagellaten. (Heidelberg, Rossler), 61 pp., 2 pls.

GRASSI, B., and FOÀ, A.

1911. Intorno ai Protozoi dei Termitidi. Nota preliminare. Rend. R. Accad. dei Lincei, Cl. Sci. Fis. Mat. e Nat., Rome, (5), 20, 725-741.

GRASSI, B., and SANDIAS, A.

1893. Costituzione e sviluppo della società dei Termitidi. (Catania Galatola), 150 pp., 4 pls.

HARTMANN, M.

1910. Untersuchungen über Bau und Entwicklung der Trichonymphen (*Trichonympha hertwigi* n. sp.). Festschr. z. Hertwigs, 1, 349-396, pls. 27-30, 3 figs. in text.

KOFOID, C. A., and CHRISTIANSEN, E. B.

1915. On binary and multiple fission in *Giardia muris* (Grassi). Univ. Calif. Publ. Zool., 16, 30-34, pls. 5-8, 1 fig. in text.

KOFOID, C. A., and SWEZY, O.

1915. Mitosis and multiple fission in trichomonad flagellates. Proc. Amer. Acad. Arts. Sci., Boston, 51, 289-378, pls. 1-8, 7 figs. in text.

LEIDY, J.

1881. The parasites of the termites. Jour. Acad. Nat. Sci., Philadelphia, (2), 8, 425-450, pls. 51, 52.

PORTER, J. F.

1897. *Trichonympha* and other parasites of *Termes flavipes*. Bull. Mus. Comp. Zool., Cambridge, 31, 48-68, pls. 1-6.

YOCOM, H. B.

1918. The neuromotor apparatus of *Euplotes patella*. Univ. Calif. Publ. Zool., 18, 337-396, pls. 14-16.

ZULUETA, A. DE

1918. Sobre la reproduction de *Dinonympha gracilis* Leidy. Trab. Mus. Nac. Cienc. Nat., Madrid, ser. Zool., 23, 15 pp., 1 pl., 6 figs. in text.

EXPLANATION OF PLATES

All drawings of *Streblomastix strix* were made with camera lucida from material stained with iron haematoxylin, with a magnification of 2500 unless otherwise stated.

PLATE 1

- Fig. 1. Ordinary trophozoite showing few turns in torsion of the body.
- Fig. 2. Contracted specimen showing centrosome and blepharoplast near together.
- Fig. 3. Giant individual not fully drawn. Note elongated rhizoplast with blob of cytoplasm surrounding blepharoplast.
- Fig. 4. Individual showing definite nuclear membrane and blob of protoplasm with chromatin cap attached to the blepharoplast.
- Fig. 5. Body slightly contracted with little torsion.
- Fig. 6. Myonemes showing heavily stained lines.
- Fig. 7. Trophozoite with considerable torsion of body.
- Fig. 8. Position of parasites in villi of intestine; attached to the mucous lining but not to the cells of the wall.
- Fig. 9. Trophozoite with greatly elongated rhizoplast.

